BANDED ADMIRALS FROM WESTERN MARYLAND: ANALYSIS OF THE *LIMENITIS (BASILARCHIA) ARTHEMIS-ASTYANAX* COMPLEX (LEPIDOPTERA: NYMPHALIDAE) AT GREEN RIDGE STATE FOREST

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Abstract. —The various forms of butterflies comprising the *Limenitis arthemis-astyanax* complex are reviewed and their genetic relationships established. Suggestions are made for distinguishing forms *albofasciata* Newcomb and *proserpina* Edwards. The species status of *arthemis* and *astyanax* is reviewed from an historical perspective. The occurrence of banded butterflies (forms *arthemis* and *albofasciata*) at Green Ridge State Forest in western Maryland is documented. Hardy-Weinberg analyses demonstrate that the observed and expected numbers of banded, partially banded, and unbanded insects closely approximate each other in three consecutive annual samples (1982–84) and in the total sample as well (n = 586). Analyses of "beak tear" frequencies among quantitative samples of banded, partially banded, and unbanded butterflies in the UMBC and Milwaukee Public Museum Collections, suggest that bird predation is an important factor driving the evolution of the disruptively banded and unbanded mimetic wing patterns north and south of the blend zone, respectively. Within the blend zone, similar data suggest that selection is "relaxed." Wing fragments obtained from 47 butterflies eaten by a single gray catbird at Green Ridge State Forest in 1982 and 1984, suggest that localized predation can be quite heavy, with a single bird consuming an average of 11 butterflies per day.

The banded purple and red-spotted purple butterflies of the northeastern United States form a fascinating complex of blending populations which are of extreme interest to students of evolution and natural selection. Despite the facts that the two parental forms look very different from one another, and that they occupy different but adjacent geographic areas, they are nonetheless extremely similar to each other in many features, and can be judged to represent merely forms within a single interbreeding species complex (Platt, 1983). This paper will review the important literature relating to these butterflies, and will examine the genetics, population biology, and selective adaptations of the intergrade population located at Green Ridge State Forest (Allegany Co.) in western Maryland. The region is part of the "Ridge and Valley" biotic area of Maryland (Fales, 1974). This population is important because it represents a southern protrusion of the northeastern *L. arthemis-astyanax* blend zone, which runs southward along the "backbone" of the Appalachians, extending into western Virginia. Apparently, Green Ridge is the only locality in Maryland where the banded admirals occur in any numbers.

Forms of the Admiral Butterflies

The *L. arthemis-astyanax* complex consists of four major forms (Table 1), each of

which will be discussed and described in turn:

1) Form *arthemis* (Drury, 1773).—This is the common and widespread northern banded purple butterfly. It is believed to be ancestral to the other forms and species within the genus (Chermock, 1950; Platt et al., 1970). The white bands are wide and conspicuous on all wings. Its geographic range extends from Alaska across Canada to Nova Scotia and southward into Pennsylvania and New England. The medial wing bands provide a disruptive color pattern of alternating dark and light fields (Platt and Brower, 1968; Platt, 1983).

2) Form *astyanax* (Fabricius, 1775).— This is the common black and iridescent blue-green butterfly, lacking bands, but having large and conspicuous red-orange spots along the ventral hindwing (VHW) margins. It is a known Batesian mimic of the unpalatable blue swallowtail (*Battus philenor* L., Papilionidae), with which its geographic range is widely co-incident (Brower and Brower, 1962; Platt et al., 1971). The subspecies *L. a. astyanax* is distributed from central New England southward to the Gulf Coast, into central Mexico, and westward across the Great Plains to Arizona.

3) Form *proserpina* (Edwards, 1865).— This butterfly is distributed across two degrees of latitude (41°–43°N) within the *arthemis-astyanax* blend zone (Edwards, 1884; Saunders, 1932; Hovanitz 1949; Platt and Brower, 1968). The type locality is the Catskill Mountains of eastern New York State (Edwards, 1865, 1873, 1877, 1891; Smith, 1891). In the central region of the blend zone, this partially banded heterozygous form usually is the most prevalent one. The form is subject to considerable phenotypic variation, running the gamut from conspicuous partial white banding on all wing surfaces to individuals having virtually no expression of the band at all. These forms have been classified as white band (WB) categories 3, 4, and 5, respectively by Platt and Brower (1968) and Platt (1975). Hence, *proserpina* continuously grades into

the *astyanax* phenotype. It is distributed from Maine across southern Ontario to extreme northeastern South Dakota, and southward into New York and Pennsylvania, as well as throughout Maryland (where it is rare), and into western Virginia. It is most prevelant within the central region of the *arthemis-astyanax* blend zone, but can occur wherever the geographic ranges of the two parental forms overlap.

4) Form *albofasciata* (Newcomb, 1907).— This form was first described to represent a white banded "*ursula*" (sic *astyanax*). The type localities of the original male and female specimens are in eastern Massachusetts. Unfortunately, the two types (presently in the USNM collection, Smithsonian Institution) now are known to represent genetically distinct phenotypes. The male (a reared specimen) possesses a distinctive, very straight and narrow, medial white band, especially evident on the hindwings. On the other hand, the female type has a somewhat wider, bowed white band, which, although narrower than normal, cannot be genetically distinguished from form *arthemis* per se. Thus, I suggest restricting the usage of form *albofasciata* (Newcomb) to apply only to those individuals having the distinctive narrow banding of the male type specimen. Such a form occurs in both sexes and breeds true. The differences between form *arthemis* and form *albofasciata* are shown in Figs. 1–4. Figs. 2 (*arthemis*) and 3 (*albofasciata*) are very close to Newcomb's original type specimens of *albofasciata*. The form *albofasciata* is rare in most populations. It occurs mainly throughout the southern one-half of the *L. arthemis-astyanax* blend zone (Platt, 1983, fig. 6, p. 18). It is common among the banded butterflies at Green Ridge in western Maryland, and it has been taken in Nelson County, and at Mountain Lake (Giles Co.), Virginia (Clark and Clark, 1951).

SPECIES STATUS OF THE
L. ARTHEMIS-ASTYANAX COMPLEX

Because they possess distinctive color patterns and geographic ranges (see above)

Dorsal

Ventral

├──────┬──────┤
     2 cm
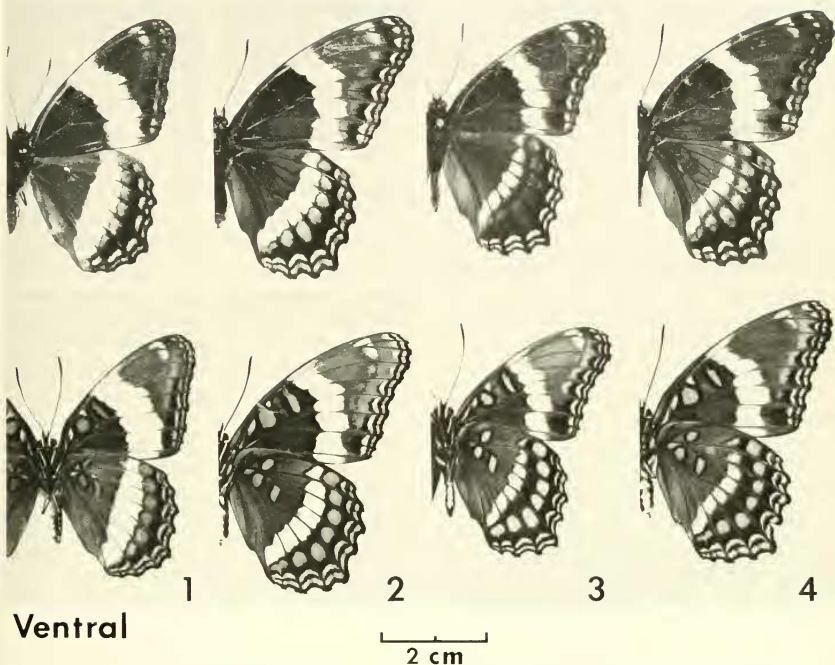
Figs. 1–4. Lab-reared F_1 specimens of banded admirals, showing the wide and narrow banded forms. The specimens are in the UMBC collection. They represent the central Massachusetts stock, but are nearly identical to those found in western Maryland. 1) & 2) ♂ & ♀ of form *L. a. arthemis* (Drury), 3) & 4) ♂ & ♀ of form *L a. albofasciata* (Newcomb). The two central specimens [2) ♀ *arthemis* (with white band slightly narrowed and bowed) & 3) ♂ *albofasciata*], closely approximate Newcomb's (1907) types of form *albofasciata*. The latter are illustrated life-sized in color on the plate accompanying the original description in *Psyche*. Both types are now in the USNM collection in Washington, D.C.

arthemis and *astyanax* were first considered to be distinct species. This antiquated view is in agreement with the original "type species" concept, based exclusively on morphology. However, the more recent (and advanced) species concepts include 1) the "non-dimensional" concept, which emphasizes the "discontinuities of nature" (e.g. that all natural species are distinctive, or different, from one another), and the "multi-dimensional" (or biological) species concept, which questions whether or not two forms are either potentially, or actually, capable

of interbreeding in the natural environment (Mayr, 1963, 1970). By either of these two latter concepts, the *L. arthemis-astyanax* butterflies must be judged to represent a single species for reasons I shall demonstrate.

Grey (1879), Edwards (1884, 1891) and Scudder (1889) recognized the seeming plasticity of these butterflies. Likewise, Field (1904, 1910) and Poulton (1909) stressed the importance of their species relationships, and what these, in turn, can tell us about the evolution of mimicry. Nakahara (1924) provided evidence that suggested that

arthemis and *astyanax* were the same species, based on his genitalic studies of all of the North American *Limenitis.* Saunders (1932) and Gunder (1934) discussed the *L. arthemis-astyanax* complex at length, stressing both the abundance and variable nature of the intergrading forms of *proserpina,* but Klots (1953) accepted the single species viewpoint. Other authors, Hovanitz (1949) and Remington (1958, 1968) have re-emphasized that they are two species, whereas, Platt and Brower (1968), Platt et al. (1970), and Platt (1975; 1983) have further stressed the single species concept.

Fisher (1958: 145–146) provided an initial interpretation of this butterfly complex, as follows:

"An example of a species in process of fission, in which sexual preference is evidently playing an important part, occurs in butterflies of the genus *Limenitis* (*Basilarchia*) in the Eastern United States . . . . The interpretation of the data is facilitated by the circumstance that the conspicuous white band in *L. arthemis* is due to a single Mendelian factor, in which that form differs from *astyanax* . . . . The white band is incompletely recessive and hybrid females caught wild and yielding 50 per cent *arthemis*-like young, have thus shown themselves to be fertile with the one parental form . . . ."

"A most important feature, the significance of which has been pointed out by the late Professor Poulton, is that the rarity of the heterozygotes, in the zone in which they occur, implies that the butterflies in this zone display a strong preference in mating, each for its own kind . . . . It is probable, in fact, that heterozygosis is here never maintained for more than a few generations, and that almost the entire supply of heterozygotes comes from stray matings of the subspecies, which are thus on the verge of complete genealogical separation."

The above interpretation is most certainly wrong, as data provided by Platt and Brower (1968), Bergman and Masters (1971), and by Platt (1983) point out. Across

the zone of intergradation between *arthemis* and *astyanax,* a north-south transect in New England (four localities) revealed that the heterozygotes (form *proserpina*) were abundant (not rare, as presumed by Fisher), and that the butterflies were, in fact, breeding at random, in accordance with the Hardy-Weinberg principle (Platt and Brower, 1968). Annual studies of the northern Vermont and central Massachusetts populations (1965–1975) have confirmed these findings. Likewise, other populations within the blend zone (e.g. those in northern and central Pennsylvania, central Wisconsin, Minneapolis, and northeastern South Dakota) also evidence "free" interbreeding just as was found for the New England localities (Platt, 1983).

Thus, the original scenario presented by Fisher (1958) is incorrect: *arthemis* and *astyanax* apparently are not "on the verge of complete genealogical separation." In fact, Platt and Brower (1968) have suggested that their relationship is one of primary intergradation, in which the two parental butterflies never have been geographically separated from each other, rather than one of secondary intergradation, following isolation, as Fisher's hypothesis assumes.

A more simple and straightforward model is that the differences between *arthemis* and *astyanax* are the result of natural selection, which factors disruptive coloration (wing banding) in the north, and mimicry (without wing banding) of *Battus philenor* in the south. The northeastern blend zone, then, can be viewed as a steep cline of selective reversal between these two forces, with the frequencies of the morphs (and alleles) of the white band (WB) adjusting themselves to the relative strengths of the two forces at any one locality, thus effectively neutralizing the "net" selection across the blend zone from north to south. This intergrade zone then may be considered to be a region of "relaxed" selection, thus, accounting for each local population being in Hardy-Weinberg equilibrium. It is, in es-

sence, a valley (or trough) between two adaptive peaks. A detailed examination of this phenomenon, as it relates to the intergrade population at Green Ridge State Forest in western Maryland follows.

METHODS AND MATERIALS

The Hardy-Weinberg (H-W) Principle. — This principle is based on a number of assumptions almost all of which do not hold precisely true when applied to natural populations of organisms. Thus, the H-W principle often is used as an hypothetical "yardstick" against which to assess mating systems in natural populations, to determine just how much they deviate from theoretical H-W predictions as a result of selective forces.

Among these assumptions are the following: 1) a single locus having two alleles controls the trait (or traits) in question; 2) random mating (panmixia) occurs between the sexes in the population; 3) no migration or immigration is occurring in the population; 4) a constant environment is assumed; and, finally, 5) no "net" selection is taking place. All of these assumptions hold only approximately at best, when applied to the *L. arthemis-astyanax* butterflies in nature.

Procedures for the H-W analyses. — The first step necessary for carrying out an H-W analysis is to obtain a quantitative "random" sample (or samples) of butterflies from one of the blending populations. This means that all insects encountered must be collected, regardless of phenotype, wing condition, or sex. Equal effort must be expended to collect each and every individual (no matter how common or rare), in the order in which they are encountered. Usually about 70% of the *Limenitis* seen can be taken with hand nets. Such samples most often are biased in favor of males, which, unlike females, tend to be territorial, and often sit in roadways for a day or so following eclosion, presumably to obtain nutrients and salts. Samples of between 30 to 100+ individuals should be collected in as brief a time period as possible. Each sample should

be obtained from as small a localized area as possible, so that it will be representative of a single deme, or localized interbreeding group.

Next the sample must be pinned and fully labeled. Each specimen is catalogued by specimen number and its complete phenotype (of four independently inherited wing color pattern characters) is recorded (see results section). The following steps are done to perform the H-W analysis: 1) Calculation of the allelic frequencies for the major gene controlling wing banding. This genetic locus will be termed the "B" (for "banding") locus. We assume that it possesses two alternative alleles, having incomplete dominance: the B_1 allele codes for wing banding and the B_2 allele codes for the unbanded condition. The H-W principle algebraically states that $p + q = 1$, and, hence, that $(p + q)^2 = 1$, as well. In this case, p equals the frequency of the "dominant" allele (e.g. B_2) and q equals the frequency of the "recessive" allele (e.g. B_1);

2) Expansion of the H-W binomial: If $(p + q)^2 = 1$ (by definition), then $p^2 + 2pq + q^2 = 1$, also. Here p^2 represents the phenotypic frequency of the "dominant" homozygotes (e.g. B_2B_2, or unbanded *astyanax*) in the population, 2pq equals the phenotypic frequency of the heterozygotes (B_1B_2, or partially banded *proserpina*), and q^2 equals the phenotypic frequency of the "recessive" homozygotes (B_1B_1 or banded *arthemis,* including form *albofasciata*);

3) Next these three phenotypic frequencies are used to generate the expected numbers of butterflies of each phenotype to be found in a sample of known size, by multiplying them by the total number of insects collected in the original sample. [In so doing, one statistical degree of freedom (df) is used up, leaving only a single degree of freedom for the chi-square analysis which follows (Srb and Owen, 1952)].

4) Finally, the observed and expected (based on the above H-W assumptions) numbers of butterflies belonging to each

Table 1. Phenotypic and genetic relationships between the four major forms of the *L. arthemis-astyanax* complex.

Morphs	*arthemis* (Drury)	*albofasciata* (Newcomb)	*proserpina* (Edwards)	*astyanax* (Fabricius)
Relative phenotypic categories (Platt & Brower, 1968)	1	2	3, 4, 5	6
Wing banding phenotypes	Full, wide	Full, narrow	Partial (visible dorsally, to trace beneath forewings only)	Absent
Genotypes	$B_1B_1M_1-M_2-$ (incompletely recessive homozygote, modifier loci dominant)	$B_1B_1m_1m_1m_2m_2$ (double, or triple recessive homozygote)	$B_1B_2-,-$ (heterozygote)	$B_2B_2-,-$ (incompletely dominant homozygote)

Note: The phenotypic relationships are as follows:

astyanax > *proserpina* > *arthemis* > *albofasciata*
(B_2B_2)   (B_1B_2)   ($B_1B_1M_1-,M_2-$)   ($B_1B_1m_1m_1m_2m_2$)

phenotypic class are compared using chi-square analysis. If the two groups of numbers closely approximate one-another, a low chi-square value will result, leading to the inference that they do not differ significantly from one another. If, on the other hand, the observed and expected numbers are disparate, a large chi-square value will result. If large enough (chi-square, ≥ 3.84), then the null hypothesis (H_0) that the observed and expected numbers do not differ significantly must be rejected at the 5% level of confidence. Then, an alternative hypothesis (H_A), e.g. that the numbers do differ significantly, will be chosen. This latter result is the one to be expected if the heterozygous phenotype (*proserpina*) is truly rare in natural populations of the *L. arthemis-astyanax* butterflies. See Speiss (1977) for further in-depth considerations of these procedures.

RESULTS

Genetic relationships of the forms.—The genetic relationships of the four common forms of the *L. arthemis-astyanax* complex are shown in Table 1. White wing banding (WB) is controlled by a single major autosomal gene having two alleles, banded (B_1) and unbanded (B_2). The alleles exhibit incomplete dominance, in and of themselves. However, the *astyanax* phenotype quite likely is evolving dominance (Clarke and Sheppard, 1960; O'Donald and Barrett, 1973; Ford, 1975) in regions where the unbanded morph prevails, through the accumulated action of unlinked modifier alleles at separate autosomal loci. The penetrance of the partial white banding in the heterozygous form *proserpina* (B_1B_2) is less on average in the southern areas of the blend zone than it is further north, in the central regions of the zone. Earlier breeding studies with insect strains from Shutesbury (Franklin Co.), Massachusetts (see Figs. 1–4) demonstrated that form *albofasciata* bred true and was recessive to form *arthemis,* as well (Platt, 1983). The differences between the two forms resulted from the action of two

separate unlinked autosomal modifier loci (M_1 and M_2, respectively). However, recent breeding experiments using insects from the Green Ridge, Maryland population, in which form *albofasciata* was recovered from heterozygous ("trace" and partially banded) parents (1984–85 unpublished data), suggest that only a single modifier locus is segregating in that strain. Perhaps the other modifying locus has become locally fixed, so that it no longer segregates. This has happened either just in my laboratory strains alone, or in the entire western Maryland population itself. Further study will be required to resolve these two possibilities.

THE INTERGRADING POPULATION AT GREEN RIDGE STATE FOREST, MARYLAND

Through verbal and written correspondence with several members of the Maryland Entomological Society (M.E.S.) I have located 21 records of banded admirals collected in Green Ridge State Forest (Allegany Co.), Flintstone Township, Maryland and the immediate surrounding areas. Most of these insects were collected along Fifteen Mile Creek Road near bridges and other areas where the adjacent stream and drainage ditches adjoin the gravel roadway. Simmons and Andersen (1961) reported the first banded admiral from Maryland. A specimen in the Carnegie Museum of Natural History in Pittsburgh, taken by the late Harry Clench, was collected in 1970 (J. E. Rawlins, pers. comm.). between 1981–1984 at least 19 other specimens have been taken, a number of them by several M.E.S. collectors, including E. Cohen, J. Fales, W. Grooms, P. Kean, and J. Zeligs. All of the specimens were collected between 10–30 June, except for one in early August. The specimens include 20 males and one wide banded female, as well as 11 *arthemis* (wide banded) and 10 *albofasciata* (a near 1:1 ratio).

The chronological collection dates of these specimens are as follows: 1) VI.30.60, 2) VI.19.70, 3–5) VI.14, 15, and VIII.6.81, 6–

14) VI.15, 16 (2), 17, 20 (3), 23, and 30.82, 15–18) VI.10, 15, 19, and 26.83, and 19–21) VI.20 (3).84. These 21 specimens have been phenotypically classified for three other wing color characters (in addition to wing banding), using the six relative category values defined by Platt and Brower (1968), and Platt (1975). These are given below:

1) Dorsal forewing marginal red-orange spotting (FWR);
2) dorsal hindwing marginal red-orange spotting (HWR);
3) dorsal hindwing blue-green iridescence (IB).

For FWR, HWR, and wing banding (WB), the six relative phenotypic categories are:

Category 1 = full expression (large, or wide);
Category 2 = full expression (small, or narrow);
Category 3 = partial expression (greater, or dorsal);
Category 4 = partial expression (lesser, or ventral only);
Category 5 = trace expression (remnant only); and
Category 6 = expression lacking

For IB the relative expression among the six phenotypic categories is exactly the reverse of those given for the three traits above. The $\bar{x} \pm$ SE values of these four traits among the 21 wild-collected banded insects from Maryland are: FWR: 5.1 ± 0.4, HWR: 5.0 ± 0.3, IB: 3.3 ± 0.2, and WB: 1.5 ± 0.1.

All three of these other traits are controlled by autosomal polygenic loci which are not correlated either to white banding, or to each other (Platt, 1975). However, the dorsal hindwing bands of one unusual example of *albofasciata* taken by W. Grooms and J. Zeligs on 23 June, 1982, are markedly suffused with iridescent blue scales, closely resembling partially banded form "*cerulea*" (Ehrmann, 1900) which exhibits this same condition ventrally.

In addition to these collected specimens, I am aware of four additional "sight" rec-

Table 2. Observed and expected numbers (the latter in parentheses) of butterflies in consecutive annual samples obtained from Green Ridge State Forest, Maryland. A) observed and expected numbers in annual samples. B) allelic frequencies and results of H-W analyses. C) G statistics: R × C tests of independence [methods of Sokal & Rohlf (1981: 745)].

A) Observed and expected numbers in the annual samples:

Annual Sample	Banded (*arthemis*; *albo-fasciata*)	Partially Banded (*proserpina*)	Unbanded (*astyanax*)	Totals
1982	2	33	2229	264
(3 days)	(1.30)	(34.37)	(228.33)	
1983	1	19	62	82
(1 day)	(1.31)	(18.29)	(62.4)	
1984	3	32	205	240
(6 days)	(1.44)	(35.04)	(203.52)	
Totals	6	84	496	586
(10 days)	(4.10)	(87.90)	(494.00)	

B) Allelic frequencies and results of the H-W analyses:

Annual Sample	Allelic Frequencies		Chi-square $(df = 1)$	Significance $(P = 0.33)$
	Unbanded (p)	Banded (q)		
1982	.930	.070	0.43	0.52 (NS)
1983	.872	.128	0.10	0.75 (NS)
1984	.921	.079	1.97	0.18 (NS)
Overall	.918	.082	1.06	0.33 (NS)

C) G tests:

Test No. & Variables	G. Value	df	Significance $(P = \quad)$
1) 3 × 3 contingency test (3 phenotypes vs. 3 annual samples)	2.93	4	0.57 (NS)
2) 2 × 3 contingency test (observed vs. expected H-W values in overall sample)	0.17	1	0.71 (NS)

NS = Not significant.

ords of banded admirals in Maryland. Three of these were made by A. Platt and P. Kean, while collecting at Green Ridge [VI.2.82, and VI.23.83(2)]. The fourth was made near Cunningham Falls (Frederick Co.) in June, 1982 by W. Cooper. This latter record suggests that banded admirals may occur elsewhere in the state as well.

These rare banded admirals always occur in company with large numbers of unbanded *astyanax,* and the somewhat less common partially banded individuals referrable to *proserpina* (the heterozygous form). The majority of the latter in Maryland have a mere trace of the partial white band. These are referrable to WB phenotypic category 5 of the Platt and Brower (1968) system. That these "trace" banded insects are true heterozygotes (genotype B_1B_2) is attested to by the fact that I have been able to recover banded forms *arthemis* and *albofasciata* from them during selective laboratory breeding studies carried out at UMBC during 1984–85. (The results of these recent studies will be reported in a future paper.)

Other *proserpina* specimens possess clear ventral expression of the partial band (WB category 4 individuals), but only a very few insects exhibit partial banding dorsally (WB category 3). However, a fine example of this latter phenotype was collected by P. J. Kean on VII.3.83 at Green Ridge. These various forms of *proserpina* are found (uncommonly) flying with *astyanax* throughout the state. Examples in my collection (and those of other M.E.S. members) come from Allegany, Frederick, Montgomery, Calvert, Carroll, Baltimore, and Dorchester counties, but *proserpina* is probably even more widespread in Maryland than these records indicate.

H-W analyses of the Green Ridge population. — Results of H-W analyses performed on the Green Ridge samples obtained between 1982 and 1984 are given in Table 2. The *L. arthemis-astyanax* butterflies were exceedingly common during 1982 and 1983. It was during these years that 13 of the 21 banded specimens were collected. Table 2A lists the observed and H-W expected numbers in each annual sample, and among the total of 586 butterflies captured. The allelic frequencies and the chi-square test results (2B), clearly indicate that the observed and expected numbers do not differ significantly from one another. $\Sigma \chi^2_1 \geq$ 0.18 in all cases, with the overall $\Sigma \chi^2_1$, value being 1.06, with $P = 0.33$).

Since the banded butterflies are so rare in

the western Maryland population, their ex- pected numbers in the H-W analyses are below five. This means that there is a high likelihood of the observed and expected numbers deviating from one another simply by chance alone. However, the data them- selves show that this has not occurred. Fur- thermore, two G tests of independence have been run on these data (Table 2C). Test 1 shows that the three annual samples are alike, and so can be pooled. Test 2 indicates that the observed and expected numbers are very close approximations of one another. Neither of these two tests yielded significant G values, with $P \geq 0.57$ in each test. The G tests are independent of the numbers in each subcategory, yet their results support the findings of the above chi-square anal- yses. Thus, I conclude that the *L. arthemis- astyanax* butterflies are breeding at random (and hence exhibit panmixia) at Green Ridge, just as they were at all of the New England localities studied earlier by Platt and Brower (1968), and at other more northern localities within the blend zone (Platt, 1983).

Among the 84 *proserpina* collected at Green Ridge between 1982 and 1984 were four WB category 3 (5%), 28 WB category 4 (33%), and 52 category 5 (62%). The H-W analyses indicate that there is no statistical deficiency of these partially banded hetero- zygotes. Thus, they form a stable part of the *astyanax* populations along the southern margin of the *L. arthemis-astyanax* blend zone, and the banded alleles are commonly carried by individuals closely approaching the *astyanax* phenotype.

Assuming panmixia and utilizing the ge- notypic frequencies of the three forms [*ar- themis* (including *albofasciata* = 0.007), *proserpina* = 0.150, and *astyanax* = 0.843], it is possible to calculate the frequency with which matings are expected to occur (by chance) between the various morphs. Of all possible matings, 71.0% should occur be- tween unbanded (*astyanax*) individuals. Another 25.3% should take place between

partially banded and unbanded insects. Only 2.3% will involve two heterozygotes (*pro- serpina*), and another 1.2% would be be- tween banded and unbanded individuals (yielding all partially banded progeny). Be- cause of the low genotypic frequencies, only one in every 500 matings will involve a banded x partially banded cross (0.20%), and the banded individuals are so rare that only one in 20,000 matings should involve two banded individuals (0.05×10^{-3}%). The rare banded individuals occurring at Green Ridge mainly result from crosses between partially banded heterozygotes (form *pro- serpina*). Such crosses are expected to yield approximately 25% banded individuals.

Selection and bird predation.—When quantitative samples of *L. arthemis-astya- nax* butterflies are obtained, certain indi- viduals possess large, jagged chunks missing from their wings. The wing condition of many of these insects is otherwise fresh. Such damage is assumed to represent "beak tears" caused by insectivorous birds chasing and attempting to catch the live butterflies (Bowers and Wiernasz, 1979). Similar dam- age has been found on wings of 47 *arthemis- astyanax* butterflies from western Mary- land, which were killed and eaten presum- ably by a male gray catbird (Mimidae: *Du- metella carolinensis*) at Green Ridge. Beak tears result from a butterfly (or moth) strug- gling and escaping from a bird that has caught it, and is holding one or more wings in its bill (Sargent, 1973, 1976; Robbins, 1980). On the other hand, "beak marks" are crisp impressions of the outlines of bird beaks, which result from a bird biting and then gaping, thus, releasing the insect (Ed- monds, 1974). Beak marks seldom are found on wings of admiral butterflies (except on wings of those that have been eaten, referred to above). They are more likely to be found on wings of unpalatable species, such as model butterflies (*Danaus, Heliconius,* etc.), which birds attack and catch, but often fail to kill or eat (Brower, 1984).

The frequency of beak tears among *L.*

Table 3. "Beak tears" among wild-collected *Limenitis arthemis-astyanax* butterflies in the UMBC and Milwaukee Public Museum collections—1982 data.

Locality and Form	Sample Size	No. and Percent of Individuals with "Beak Tears"
So. Quebec and No. Vermont		
arthemis	263	81 (30.8%)
Central Mass. intergrades		
arthemis	155	10 (6.5%)
proserpina	376	28 (7.5%)
astyanax	351	34 (9.7%)
Subtotals	882	72 (8.2%)
Central Wisconsin		
proserpina (M.P.M.)	76	16 (21.1%)
Southern *astyanax*		
(CT, RI, NJ, VA,		
W.MD, IL)	373	42 (11.3%)

arthemis-astyanax butterflies in the UMBC collection, and in a sample of *proserpina* borrowed from the Milwaukee Public Museum, is given in Table 3. The Vermont, Massachusetts, and southern (*astyanax*) samples have been collected "at random" by me during June and early July. They are comparable in terms of butterfly condition and age. I assume that the beak tear frequencies shown in the table reflect differential predator intensity between localities. These analyses reveal that about 30% of the disruptively banded northern *arthemis* butterflies exhibit beak tears, whereas only about 11% of the mimetic unbanded southern *astyanax* have similar damage. In central Massachusetts (within the central region of the zone of intergradation) only 8.2% of 882 butterflies examined exhibit such damage, and the frequency of this damage is not significantly different between the three insect forms ($\Sigma \chi^2_2 = 1.81$, $P > 0.33$). In central Wisconsin, 21.1% of a sample of form *proserpina* (n = 76) showed beak tears. Among 234 beak tears on the wings of *L. arthemis-astyanax* butterflies analyzed (all samples pooled), 68% were on the hindwings (Type I damage), 27% were on the forewings (Type II damage), and only 5% of the beak tears involved both fore- and hindwings (Type III damage) together. This system of categorization is modified from one used by (Sargent 1976) for noctuid moths (*Catocala* spp.). Some individuals in Table 3 contained several separate beak tears. Attacks occurred from either the left or right sides with equal frequency.

My interpretations of the beak tear data are based upon the assumption that the frequency of beak tears on the insect wings reflects true attack rates of birds on the butterflies themselves. If this is true, then the differences in beak tear damage shown by the samples in Table 3 represent actual differences in the attack rates by birds on the butterflies in the different geographic regions. What such damage is measuring, in reality, are successful butterfly escapes from bird attacks. The missing information is just how many butterflies of each form are caught and eaten by birds.

Some light can be shed on this problem by examination of wing fragments collected by P. J. Kean and myself at Green Ridge on VI.20 and VI.23, 1982. Separate wings of 13 males (four *proserpina,* eight *astyanax*) were collected from a single locality on the first day. A male gray catbird was flitting about the adjacent shrubbery, near where a large "mud-puddle club" of male butterflies had aggregated at the edge of the roadway. Crisp beak marks, sharp and V-shaped, as well as numerous beak tears, were found on the insect wing fragments. The outline of the beak marks, including a sharp pin-like hole at the tip of the "V," matched the outline of a catbird's beak perfectly. Three days later, wing fragments of 33 additional insects were recovered at the same area, and the male catbird still was very much in evidence. The bird apparently was feeding heavily on a locally abundant and easily obtainable food supply, and was consuming an average of 11 butterflies per day. The butterflies evidently were being caught while sitting on the gravel roadway,

where they could easily be closely ap-
proached, even by humans. Two years later,
VI.20.1984, wing fragments of two addi-
tional butterflies, one an *astyanax* and the
other a banded form *albofasciata,* were col-
lected at precisely the same locality. This
evidence indicates that birds at times will
prey on the adult admiral butterflies, es-
pecially when they are common, and it sug-
gests that the damage termed "beak tears"
is, in fact, caused by birds attacking the live
butterflies. Such attacks can occur either
when a butterfly is perching or sitting on a
roadway (as above), or when the insect is
flying. The author has witnessed three un-
successful bird pursuits of flying *arthemis*
butterflies over the years. Two occurred in
northern Vermont, and involved a gray cat-
bird and a barn swallow (Hirundinidae: *Hi-
rundo rustica*). The other occurred in central
Massachusetts, and involved a blue jay
(Corvidae: *Cyanocitta cristata).*

Discussion and Conclusions

The evidence taken in its entirety sup-
ports the contention that the *L. arthemis-
astyanax* zone of intergradation is main-
tained by the counter-balancing selective
forces of disruptive coloration and mimic-
ry, as postulated by Platt and Brower (1968).
The driving forces behind the evolution of
both the banded and unbanded morphs is
very likely differential predation by birds.
Throughout the blend zone selection is "re-
laxed," since these two opposing forces are
in balance with one another. The banded
and unbanded allelic frequencies adjust
themselves to the relative strengths of the
two forces at any one locality, resulting in
a situation of no "net" selection. The but-
terflies clearly are breeding at random with
one another throughout the blend zone. Both
males and females apparently totally dis-
regard wing banding phenotype in choosing
their mates. Because no "net" selection oc-
curs across the zone of intergradation, local
populations remain in Hardy-Weinberg
equilibrium. The entire complex, therefore,

must be regarded as a single polymorphic,
biological species. North of the blend zone
the banded *arthemis* form prevails, where-
as, southward, where the model species is
abundant, unbanded mimetic *astyanax* are
favored. As the unbanded morph evolved,
the banded alleles have become "masked,"
or covered up, by the action of unlinked
modifier loci. That the alleles have not been
"lost" from the *astyanax* populations is im-
portant. Within the blend zone, the partially
banded form *proserpina* more or less "strad-
dles the fence." It provides a genetic link
between the two unlike parental morphs.
The presence of variable phenotypes within
the intergrade populations, possibly serves
to confuse bird predators, by keeping them
from becoming specialists on any one
morph, and perhaps, causing them to seek
alternative prey species a higher proportion
of the time.

Acknowledgments

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NOTE

New records of *Brachydeutera* (Diptera: Ephydridae) in Malaysia

During a recent trip to Malaysia I was able to collect several small series of *Brachydeutera* from throughout the country. As the genus was recently revised for the Oriental Region (Mathis, W. N. and K. D. Ghorpadé. 1985. Smiths. Contr. Zool. 406: 1–25) it is appropriate to add some additional distributional information. Three species were encountered with *B. pleuralis* Malloch representing a new record for Malaysia.

Brachydeutera hardyi Wirth was found both in peninsular and East Malaysia, but in low numbers. In Sabah State (2 ♂♂, 6 ♀♀; Tawau, pond shoreline, 6 Nov 1986) it was collected from the surface of a shallow drainage pool which was subject to periods of extreme flooding. The pool had a grass base. In Perak State (MARDI-Hilir Perak, 16 mi W Telok Anson, 26 Nov 1986) only two females were obtained from the surface of a small, rain-fed drainage ditch. This ditch had a mud and sand base with little emergent vegetation. *Brachydeutera hardyi* shared this habitat with *B. longipes* Hendel.

Brachydeutera longipes Hendel was collected in Perak State (1 ♂, 1 ♀; same as above except 25 Nov) and in large numbers in Melaka State (46 ♂♂, 83 ♀♀; Kg. Gadek, nr Alor Gajah, 19 Nov 1986). The Melaka habitat consisted of numerous small, rainfed depressions which were 3–10 cm in depth. The pools had a grass base and also were susceptible to periods of drying and flooding.

Brachydeutera pleuralis Malloch represents a new record for Malaysia but was collected only in Kelantan State (13 ♂♂, 22 ♀♀; Bachok, shallow pool, 16 Nov 1986). This species was taken from the surface of numerous sandy, shallow pools which were several hundred meters from the coastline. The pools were 2–30 cm deep and contained no macro-vegetation. There was little macro-vegetation surrounding the pools that were bordered on both sides by large dunes. The water showed no signs of salinity.

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